African Invertebrates Vol. 44 (1) Pages 203–212 Pietermaritzburg August, 2003

Lineage mosaics in millipedes

by

Robert Mesibov

(Queen Victoria Museum and Art Gallery, Wellington Street, Launceston, Tasmania,
Australia 7250; mesibov@southcom.com.au)

ABSTRACT

Allopatric/parapatric distribution mosaics are apparently widespread among millipede genera, notably in Polydesmida. In this paper I discuss possible origins for these lineage mosaics and possible mechanisms for the persistence of their narrow parapatric zones, using mainly Tasmanian examples. Although it seems unlikely that lineage mosaics arise through rapid differentiation of a single widespread ancestor following vicariance partitioning of its range, it will not be possible to test competing hypotheses of origin and persistence in lineage mosaics until more genetic data become available, especially sequence data from intensively sampled areas.

INTRODUCTION

Mosaic complexes of millipedes have 'large generic distributions, limited component ranges, tightly fitted parapatry patterns with limited instances of sympatry, clustering of components, and slight or minor differences between some species' (Shelley 1990*b*). The quote describes *lineage mosaics*, i.e. spatial mosaics of closely related species which are the result of differentiation in form and geographical space within monophyletic clades. Lineage mosaics in North American millipedes have been documented by Shelley (1990*a*) and Shelley & Whitehead (1986) (for smaller mosaics see also Shelley 1993 1995 1996*a* 1996*b* 1997 2001), and seem to occur also in South African Spirostreptida (Hamer & Slotow 2000), Japanese Polydesmida (Tanabe & Shinohara 1996) and New Zealand Polydesmida (Johns 1979). Two lineage mosaics have been reported in Tasmanian Polydesmida (Mesibov 2003*a*,*b*) and at least eight others have become apparent in the course of sorting and mapping undescribed Tasmanian species (Table 1).

Shelley (1990*a*) wondered why so many millipedes form mosaic complexes, and how the process occurs. In this paper I discuss possible mechanisms for mosaic differentiation in millipedes, paying special attention to species overlap zones. Most of my examples are Tasmanian, but the discussion is general and will hopefully encourage others to look closely at millipede mosaics elsewhere in the world.

DISCUSSION

Mosaic boundaries

Overview of parapatry

Perhaps the most striking features of millipede mosaics are their internal boundaries, i.e. the narrow parapatric zones where two species ranges meet and overlap. Parapatric zones are not uncommon among terrestrial invertebrate species, having been documented in groups as diverse as ants (Wehner *et al*. 1994), beetles (Sota *et al*. 2000), butterflies (Porter *et al*. 1994), grasshoppers (Key 1982 1991; Orr *et al*. 1994), land snails

(Schilthuizen 1994; Shimizu & Ueshima 2000) and velvet worms (Mesibov & Ruhberg 1991). Some carefully mapped zones have been found to be remarkably narrow, e.g. <50 m for two Tasmanian velvet worms (Mesibov & Ruhberg 1991), *ca* 100 m for millipedes in Japan (Tanabe & Shinohara 1996) and Tasmania (Mesibov, unpublished results), and <200 m for Indonesian grasshoppers (Bridle *et al*. 2001).

Parapatric zones are generally thought of as stable in a biogeographical sense. In other words, although a zone may move across the landscape (Bull & Burzacott 2001), it is not merely a stage in the development of extensive sympatry. The persistence of parapatric zones has been explained in four general ways, which I here call the *overlapping limits*, *hybridisation*, *competition* and *controlling factor* hypotheses. A fifth explanation, here called *false parapatry,* is available for species which appear to have contiguous ranges at coarse map scales, but which are actually allopatric, being separated by a narrow dispersal barrier or 'no-man's land' (scorpions: Gantenbein *et al*. 2000; butterflies: Shapiro 1992). Two congeneric polydesmidan species in eastern Tasmania may be falsely parapatric (Mesibov 2003*b*); their ranges extend into, but apparently do not meet in the valley of the Little Swanport River.

TABLE 1.

Prevalence of lineage mosaics in Tasmanian Polydesmida. Genera listed include about half the species so far recognised (Mesibov 2000); unpublished names are disguised. 'Yes (part)' means that at least one species in the genus is widespread and sympatric with some congeners; see Mesibov (2003*a*) for an example.

Genus	**No. of species**	**Mosaic?**
Dalodesmidae		
Genus 'Atal'		
- (epigeal species)	2	Yes
Australopeltis	17	Yes (part)
Genus 'Dasy'	4	Yes
Gasterogramma	8	Yes (part)
Lissodesmus	3	Yes
Genus 'Rank'	4	Yes
Tasmaniosoma	14	Yes (part)
Tasmanodesmus	1	Not applicable
Genus A	4	Yes
Haplodesmidae		
Asphalidesmus	2	No (widely disjunct)
Paradoxosomatidae		
Genus 'Athe'	1	Not applicable
Dicranogonus	1	Not applicable
Notodesmus	1	Not applicable
Pogonosternum	2	No (widely disjunct)
Somethus	2	No
Family uncertain		
Genus C	7	Yes (part)
Genus D	4	Yes

Overlapping limits

Imagine a species A which prefers the low end of an environmental gradient in the landscape, and which reaches the limit of its environmental tolerance at point X on a spatial profile of the gradient (Fig. 1). A second species B prefers the high end of the gradient and

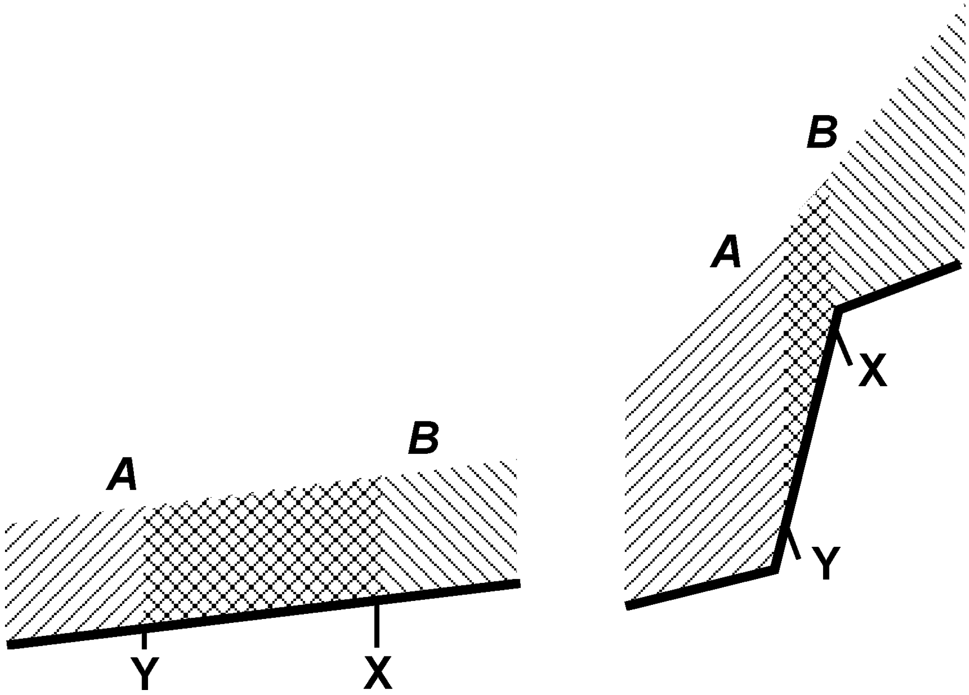

Fig. 1. Diagrammatic representation of overlapping limits parapatry on a gradual (left) and steep (right) environmental gradient. Species A extends up-gradient to its environmental limit at X, while species B extends down-gradient to Y. The width of the overlap zone varies with the steepness of the gradient.

ranges to a limit at Y, which is down-gradient from X. If the gradient is steep, for example at a sharply defined ecotone, the A–B overlap zone will be narrow. If the gradient is gradual, A and B may overlap considerably. Given a stable gradient and stable tolerance limits, the overlap zone should also be stable. There is no requirement in this hypothesis for A and B to be closely related, or for the two species to interact in any way. Their overlap zone is an ecological coincidence. Haffer (1986) labels this situation 'ecological parapatry' as distinct from 'competition parapatry', but Bull (1991) argues that 'some form of biological interaction is probably required to prevent expansion into the less favorable habitat, except at extreme ecotones.' Overlapping limits parapatry in millipedes may thus also involve some form of competition (see below). A possible example of overlapping limits parapatry is represented by the two polydesmidans *Lissodesmus adrianae* Jeekel, 1984 and *L. alisonae* Jeekel, 1984 in northeast Tasmania (Mesibov 1997). The former species seems to prefer wetter habitats than the latter, and there is a variably steep rainfall gradient in that part of northeast Tasmania where both species occur. Where the moisture gradient is particularly steep, near Weavers Creek, the overlap zone is less than 250 m wide; elsewhere the zone widens to 5 km. The two species are probably not congeneric (Mesibov, in preparation).

Hybridisation

Where the ranges of two closely related forms meet, a hybrid zone may exist in which the two forms mate to produce no fertile offspring, or offspring with reduced fertility. The literature on hybrid zones has grown very large over the past 20 years, and some of the early understandings of how they function (Hewitt 1988) are now regarded as too simple (Jiggins & Mallet 2001). From a biogeographical point of view, the question is how hybridisation can generate narrow parapatric zones. The basic explanation is that isolated individuals of one form can only disperse into the range of the other form up to a certain distance. Their offspring (if any) will not be able to extend the penetration because they are most likely to be hybrids with reduced fitness. The width of the overlap zone is thus dependent in a complex way on dispersal, reproductive behaviour and genetics. Because many hybrid zones have been found to occur at ecotones, it has long been supposed that hybridisation parapatry is reinforced by competition, i.e. each form is better adapted to conditions on its side of the overlap zone than is the other form. A recent mathematical model combining the effects of reduced gene flow and interspecific competition successfully generates narrow parapatry, but only on environmental gradients; the overlap zone sits where the gradient is steepest (Case & Taper 2000).

A variably narrow hybrid zone in the chordeumatidan millipede genus *Rhymogona* in Europe has been documented by Pedroli-Christen (1990), and genetic work on the genus (Scholl & Pedroli-Christen 1996) has begun using allozyme electrophoresis. To the best of my knowledge, the only analyses of congeneric millipede relationships based directly on gene sequences (using mitochondrial DNA) are being carried out in Jamaican Spirobolida (Bond & Sierwald 2002), Japanese Polydesmida (Tsutomu Tanabe, *pers. comm.*) and Canarian Julida (Isabel Sanmartin Bastida, *pers. comm.*). In no case has there yet been a spatially intensive analysis of a hybrid zone. No morphologically obvious hybrids have so far been noted in the Tasmanian millipede fauna; hybrid zones, if they exist, will best be studied by using molecular techniques to determine the extent of introgression in the neighbourhood of parapatric boundaries.

Competition

A narrow parapatric boundary may exist between two species A and B (which are not necessarily related), because each excludes the other through competition for resources. Although this is a simple notion with a history at least as old as Darwin's idea of a 'struggle for existence,' it is remarkably hard to demonstrate unambiguously in the field, and much of the published work on competition-maintained range boundaries describes modelling and its results (Bull 1991; see also Hybridisation, above). It is particularly difficult to argue for what Haffer (1986) calls 'competition parapatry' in the case of millipedes, which seem to be relatively unspecialised detritivores sharing an abundant litter resource. A single patch of forest floor in Tasmania, for example, may be home to equal-sized juveniles or adults of 5–10 species of similar Polydesmida. Controls other than resource availability seem likely to restrict population sizes in this situation, and interspecific competition may thus be avoided. Where resources are limited, however, competition could be expected to be more intense. We might therefore expect to find parapatric boundaries lining up with sharp ecotones and with low-fertility zones within forests. In Tasmania this is sometimes, but not always the case; some narrow parapatric boundaries are in seemingly uniform, litter-rich forests (for an example, see Mesibov 2003*a*) or in broad ecotones. Nevertheless, there is an intriguing instance of narrow parapatry in northeast Tasmania between the unrelated polydesmidans *Tasmanodesmus hardyi* Chamberlin, 1920 and '*Lissodesmus*' sp. NE1 (Mesibov 1997), which are morphologically close (and distinct from all co-occurring polydesmidans) in size, colour, paranotal shape and leg form (unusually thin). If these two species are ecological equivalents, they may indeed be competing in their densely forested overlap zone.

Controlling factor

Controlling factor parapatry arises when a widespread predator, parasite or disease differentially excludes one species in an overlap zone. Although cases of this kind are known, it is not obvious how the operation of a controlling factor can maintain a stable parapatric boundary (Bull 1991). No information on possible controlling factors is available for any of the known millipede mosaics, in Tasmania or elsewhere.

Boundaries in mosaics

It would be simplistic to suppose that all the internal boundaries in a millipede mosaic persist for the same reason. It is even conceivable that the parapatric zone between two forms in a mosaic involves hybridisation at one location (where the two forms are still able to mate) and no hybridisation at another (where pre-mating reproductive isolation has developed). At all locations the problem for an investigator is to devise methods which can unambiguously rule out one or more hypothetical explanations for narrow parapatry. Unfortunately, no such methods currently exist. Even an apparently clear result, evidence for introgression across the overlap zone, does not exclude the possibility that the parapatry is largely due to competition, not hybridisation. Evidence for hybridisation parapatry in such a case would need to be sought in studies of hybrid fitness.

A remarkable feature of Tasmanian millipede mosaics is that many of their internal boundaries are congruent (for at least part of their lengths) with *faunal breaks*, which are narrow landscape zones across which invertebrate assemblages change significantly (Mesibov 1994 1996 1997 1999). There appear to be several cases in which a faunal break includes parapatric zones for both millipedes and other invertebrates, but there is, again, no reason to conclude that parapatry at a faunal break always has the same causal basis, regardless of the taxa involved.

Origins of millipede mosaics

The taxon cycle suggestion

Neither Shelley (1990*a*,*b*) nor Shelley & Whitehead (1986) explicitly proposed an evolutionary hypothesis to explain how millipede mosaics arise. However, in their discussion of *Sigmoria* Shelley & Whitehead (1986) suggest that a single species might expand its range substantially, then rapidly differentiate into geographically coherent daughter forms following vicariance partitioning of its range. Over time these forms may progressively go extinct, until the last representative of the clade is a geographically restricted species which is clearly not closely related to any other extant millipede. Repeated, out-of-phase operation of this ‘taxon cycle’ in different lineages might explain what we find worldwide: ‘Does much of today’s global diplopod picture reflect stages in the formation and breakdown of mosaics, with some genera in expansion phases, others, like *Sigmoria* and *Eurymerodesmus*, near their zeniths, and still others in periods of decline, with significant anatomical and geographical discontinuities resulting from extinctions?' (Shelley 1990*a*). Shelley & Whitehead (1986) even suggest a pace for the process: 'This implies that the history of *Sigmoria* is quite brief, perhaps post-Pleistocene. We infer a continuous, widespread, geographically varied ancestor in rather recent times...'

There are some conceptual difficulties with this picture. The first is that the mosaic ancestor has to expand its range to cover much of the area eventually occupied by its descendants. Unless the ancestor is exploiting a previously unoccupied niche or is an unusually successful competitor, it is hard to imagine how it can spread into areas already occupied by millipedes which are presumably its close relations. The 'widespread ancestor' notion makes more sense if a single species is expanding into an unoccupied landscape, such as a post-glacial one, or if the species is taking advantage of the disappearance of a dispersal barrier to invade 'new' country. In that case, however, we might expect the mosaic-making process to begin in many lineages at more or less the same time, and there would be many in-phase taxon cycles. Another potential difficulty with the idea of post-Pleistocene expansion of the mosaic ancestor is that much of the North American area in which Shelley documented millipede mosaics was not covered by ice during the Last Glacial, and formerly ice-covered areas in the northern USA are not known to be rich in mosaics. A more plausible interpretation is that vicariance partitioning, if it occurred, happened in glacial refugia, and that the mosaic ancestor became widespread (how?) *before* the Pleistocene.

Shelley's picture is also constrained by its reliance on a single mechanism for the evolution of new forms, namely vicariance partitioning of an existing range, and allopatric speciation. There is no *a priori* reason to reject other speciation mechanisms in the origin of mosaics. Parapatric speciation on an environmental gradient could produce daughter species able to exploit neighbouring, previously unfavourable habitat. Parapatric or sympatric speciation might also be driven by sexual selection, generating new mosaic 'tiles' through mating incompatibility. Even peripatric (i.e. allopatric) speciation could result in two species, only one of which occupies the bulk of the ancestral range, while the other expands into new territory. If speciation mechanisms other than vicariance partitioning are allowed, mosaics could be imagined to develop incrementally ('tile' by 'tile') in unpredictable directions, occupying a larger and larger overall range. 'As far as simple biogeographic arguments go, it may not matter much whether divergence is sympatric or allopatric. In both cases, differences are likely to first become established in some limited region, and to spread out from there. The net pattern would then be independent of the original process' (Barton 1988).

Clues from genetics and biogeography

In the absence of fossils, molecular evidence may help to clarify the mechanism of mosaic differentiation. Vicariance partitioning of the range of a widespread ancestral taxon in a 'quite brief' period should give rise to something close to a polytomy in a cladistic analysis, whereas incremental mosaic development would be reflected in a better-resolved tree, with some species pairs (recent splits) very well separated from other lineages (much older splits). Given the usual caveats, molecular clock estimates could also be used as evidence to determine whether a given mosaic developed quickly over a large area, or slowly, with different parts of the mosaic differentiating at widely different times. Finally, extensive sampling may reveal historical directionality in mosaics, either in evidence for gene flow from one place to another, or in a spatial gradient from ancestral to more derived sequences.

Another line of evidence is geographical pattern. Vicariant range partitioning should generate mosaics in which a given form is more closely related to neighbouring forms than it is to more distant forms. This is clearly not the case in the well-demarcated *Gasterogramma* mosaic in Tasmania (Mesibov 2003*a*), the components of which are divisible on gonopod form into two distinct subgeneric groups with a spatially mixed distribution across the mosaic. Relationships in other reported millipede mosaics do not seem to be so obvious; here again, molecular evidence will be useful in clarifying evolutionary pathways.

Different lineages divide Tasmania into spatially different mosaics (Mesibov 2003*a,b*, unpublished results). If vicariance partitioning was a sufficient explanation for the origin of these mosaics, we could expect the mosaics to be spatially congruent. Lack of congruence in 'tiling' from mosaic to mosaic suggests that vicariance partitioning is not an adequate explanation, or (improbably) that a series of vicariant events each created a spatially unique mosaic in one particular lineage, leaving other lineages unaffected.

The existence of faunal breaks in Tasmania (see above) suggests that certain discrete landscape zones have been influential in promoting evolution in a range of terrestrial invertebrate groups, perhaps by acting as temporary dispersal barriers promoting allopatric speciation. Preliminary mapping shows that many of the parapatric boundaries in the Tasmanian Polydesmida mosaics are congruent for at least part of their lengths, and that these congruent portions often lie along faunal breaks (Mesibov, unpublished results; note that not all faunal breaks coincide with millipede parapatric boundaries, and that not all the congruences in such boundaries coincide with faunal breaks). These spatial congruences hint that at least some of the 'tile-forming' in different mosaics was synchronous. In this view, 'tile-forming' might proceed at different paces and in different places in different mosaics, with occasional climatic and/or geomorphic events (in the neighbourhood of today's faunal breaks) generating tile boundaries in several mosaics in the same place and at the same time.

Reticulation

An issue only briefly considered by Shelley & Whitehead (1986) is hybridisation in mosaics and its evolutionary correlate, reticulation. With vicariance partitioning of the range of a formerly widespread ancestor, secondary contact might bring together a pair of forms at any stage in the development of reproductive isolation. Two well- or partly isolated forms might each simply be represented as a mosaic 'tile' following contact. Poorly isolated forms might combine to produce a geographically differentiated but potentially panmictic metapopulation, or might hybridise to produce a new, third form near the contact zone. These scenarios could also apply following range expansion by one or more species in an incrementally differentiated mosaic. Interestingly, a possible hybrid polydesmidan, *Lissodesmus* sp. NE3, has been collected in and near the parapatric zone of two putative parents in northeast Tasmania (Mesibov 1997); its hybrid status will be tested genetically.

In any mosaic, repeated hybridisation will create an incongruence between morphological characters and geography, as seen in *Sigmoria* in the USA (Shelley & Whitehead 1986) and *Parafontaria* in Japan (Tanabe *et al*. 2001), although homoplasy could conceivably produce similar results. Extensive hybridisation thus has the potential to undermine attempts to reconstruct phylogeny using morphology alone. In some cases it may be possible to deduce past hybridisation of allopatric species from a careful examination of mtDNA lineages (Shimizu & Ueshima 2000).

Taxonomic boundaries

Shelley & Whitehead (1986) used geographic coherence of component taxa as a guide to splitting *Sigmoria*. Tanabe & Shinohara (1996) applied the same reasoning in their revision of *Xystodesmus*, first seeking 'pheno-geographic units' of phenetically and geographically close populations, then 'Based on the geographical distribution and the similarity among these units, we decided whether each unit warranted recognition as a species. In this decision we also paid attention to the stability of classification'.

In cases where characters and geography are congruent (as in most Tasmanian mosaics), it is easy to decide that each 'tile' is occupied by a distinct taxonomic unit. However, in Shelley & Whitehead (1986) and Shelley (1990*a*) we find doubts as to whether mosaic boundaries separate subgenera, species, subspecies or races. Part of the uncertainty can be traced to the authors' loyalty to the biological species concept: a species must be reproductively isolated to be 'real.' Unfortunately, the sympatry test for reproductive isolation cannot be applied to an allopatric/parapatric mosaic except in its narrow overlap zones, where (as discussed above) a taxon boundary might be maintained through hybridisation, i.e. incomplete isolation.

A more productive approach is to apply the evolutionary species concept. Within each mosaic, a species is 'a single lineage of ancestral descendant populations of organisms which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate' (Wiley 1978). In this view, each mosaic component is a separate species, and will remain a species unless and until it recombines with another mosaic component in a hybridisation event. If genetic analysis demonstrates, as seems likely, that mosaic differentiation in the past has been largely irreversible, then the evolutionary species approach is justified as a guide both to erecting classifications and to deducing phylogenies.

CONCLUSION

We still do not have good explanations of how lineage mosaics form or how they are maintained, and we are not likely to make any progress on these problems until particular millipede mosaics are analysed genetically using a range of mitochondrial, and preferably also nuclear gene sequences. However, the notion that mosaics arise through rapid differentiation of a single widespread ancestor already seems unlikely, and in conflict with biogeographical evidence from Tasmanian lineage mosaics. To the simpler question 'Are allopatric/parapatric mosaic complexes widespread in the Diplopoda?' (Shelley 1990*b*), the answer for Tasmania is yes, in two senses. Mosaic distributions are the norm for lineages in the Polydesmida, which dominate the Tasmanian millipede fauna (Mesibov 2000). Mosaics are also common in geographical space. They are stacked on the map of Tasmania so thickly that any one locality is likely to be included in 5–10 mosaics. Because mosaics partition the map in different ways, and because many components have small ranges, it would be possible to show the *ca* 64 000 km^2 of Tasmania's main island as divided into a large number of polydesmidan districts, each with its own species list. Mosaic differentiation not only affords insights into millipede evolution; it spectacularly highlights the fine-scale spatial element in biodiversity.

ACKNOWLEDGEMENTS

I am grateful to the Plomley Foundation for financial assistance and to Henrik Enghoff and Tsutomu Tanabe for constructive comments on a draft of this paper.

REFERENCES

Barton, N. H. 1988. Speciation. *In*: Myers, A. A. & Giller, P. S., eds, *Analytical Biogeography. An integrated approach to the study of animal and plant distributions*. London: Chapman & Hall pp. 185–218.

Bond, J. E. & Sierwald, P. 2002. Cryptic speciation in the *Anadenobolus excisus* millipede species complex on the island of Jamaica. *Evolution* **56** (6): 1123–1135.

Bridle, J. R., Garn, A.-K., Monk, K. A. & Butlin, R. K. 2001. Speciation in *Chitaura* grasshoppers (Acrididae: Oxyinae) on the island of Sulawesi: colour patterns, morphology and contact zones. *Biological Journal of the Linnean Society* **72**: 373–390.

Bull, C. M. 1991. Ecology of parapatric distributions. *Annual Review of Ecology and Systematics* **22**: 19–36.

Bull, C. M. & Burzacott, D. 2001. Temporal and spatial dynamics of a parapatric boundary between two Australian reptile ticks. *Molecular Ecology* **10**: 639–648.

Case, T. J. & Taper, M. L. 2000. Interspecific competition, environmental gradients, gene flow, and the co-evolution of species' borders. *The American Naturalist* **155**: 583–605.

Gantenbein, B., Fet, V., Barker, M. & Scholl, A. 2000. Nuclear and mitochondrial markers reveal the existence of two parapatric scorpion species in the Alps: *Euscorpius germanus* (C. L. Koch, 1837) and *E. alpha* Caporiacco, 1950, stat. nov. (Euscorpiidae). *Revue Suisse de Zoologie* **107**: 843–869.

Haffer, J. 1986. Superspecies and species limits in vertebrates. *Zeitschrift für Zoologische Systematik und Evolutionsforschung* **24**: 169–190.

Hamer, M. & Slotow, R. 2000. Patterns of distribution and speciation in the genus *Doratogonus* (Diplopoda: Spirostreptidae). *In*: Wytwer, J. and Golovatch, S., eds, *Progress in Studies on Myriapoda and Onychophora. Fragmenta Faunistica,* Supplement **43**: 295–311.

Hewitt, G. M. 1988. Hybrid zones – natural laboratories for evolutionary studies. *Trends in Ecology and Evolution* **3**: 158–167.

Jiggins, C. D. & Mallet, J. 2000. Bimodal hybrid zones and speciation. *Trends in Ecology and Evolution* **15**: 250–255.

Johns, P. M. 1979. Speciation in New Zealand Diplopoda. *In*: Camatini, M., ed., *Myriapod biology*. London: Academic Press pp. 49–57.

Key, K. H. L. 1982. Species, parapatry, and the morabine grasshoppers. *Systematic Zoology* **30**: 425–458.

——— 1991. On four endemic genera of Tasmanian Acrididae (Orthoptera). *Invertebrate Taxonomy* **5**: 241–288.

Mesibov, R. 1994. Faunal breaks in Tasmania and their significance for invertebrate conservation. *Memoirs of the Queensland Museum* **36**: 133–136.

——— 1996. Invertebrate Bioregions in Tasmania. Report to the Tasmanian RFA Environment and Heritage Technical Committee, December 1996. Hobart:Forestry Tasmania. (online: www.rfa.gov.au/rfa/tas/raa/other/invert/index html)

——— 1997. A zoogeographical singularity at Weavers Creek, Tasmania. *Memoirs of the Museum of Victoria* **56**: 563–573.

——— 1999. The Mersey Break: an unexplained faunal boundary on the north coast of Tasmania. *In*: Ponder, W. and Lunney, D. eds, *The Other 99%. The conservation and biodiversity of invertebrates*. *Transactions of the Royal Zoological Society of New South Wales*. Mosman (NSW): Royal Zoological Society of New South Wales pp. 246–252.

——— 2000. An overview of the Tasmanian millipede fauna. *The Tasmanian Naturalist* **122**: 15–28.

——— 2003*a*. The millipede genus *Gasterogramma* (Diplopoda: Polydesmida: Dalodesmidae) in Tasmania, Australia, with descriptions of seven new species. *Memoirs of Museum Victoria* (in press).

——— 2003*b*. A new genus of Tasmanian millipede (Diplopoda: Polydesmida: Dalodesmidae) with unusual spiracles and a mosaic distribution. *Memoirs of Museum Victoria* (in press).

Mesibov, R. & Ruhberg, H. 1991. Ecology and conservation of *Tasmanipatus barretti* and *T. anophthalmus*, parapatric onychophorans (Onychophora: Peripatopsidae) from northeastern Tasmania. *Papers and Proceedings of the Royal Society of Tasmania* **125**: 11–16.

Orr, M. R., Porter, A. H., Mousseau, T. A. & Dingle, H. 1994. Molecular and morphological evidence for hybridization between two ecologically distinct grasshoppers (*Melanoplus sanguinipes* and *M. devastator*) in California. *Heredity* **72**: 42–54.

Pedroli-Christen, A. 1990. Field investigations on *Rhymogona cervina* (Verhoeff) and *Rhymogona silvatica* (Rothenbuehler) (Diplopoda): morphology, distribution and hybridization. *In*: Minelli, A., ed., *Proceedings of the 7th International Congress of Myriapodology*. Leiden: E. J. Brill pp. 27–43.

Porter, A. H., Schneider, R. W. & Price, B. A. 1994. Wing pattern and allozyme relationships in the *Coenonympha arcania* group, emphasising the *C. gardetta-darwiniana* contact area at Bellwald, Switzerland (Lepidoptera, Satyridae). *Nota Lepidopterologica* **17**: 155–174.

Schilthuizen, M. 1994. Reproductive isolation in snails of the genus *Albinaria* (Gastropoda: Clausiliidae). *Biological Journal of the Linnean Society* **52**: 317–374.

Scholl, A. & Pedroli-Christen, A. 1996. The taxa of *Rhymogona* (Diplopoda: Craspedosomatidae): a ring species. Part one: genetic analysis of the population structure. *In*: Geoffroy, J.-J., Mauriès, J.-P. & Nguyen Duy-Jacquemin, M., eds, *Acta Myriapodologica. Mémoires du Muséum national d'Histoire naturelle, Paris* **169**: 45–51.

Shapiro, A. M. 1992. Twenty years of fluctuating parapatry and the question of competitive exclusion in the butterflies *Pontia occidentalis* and *P. protodice* (Lepidoptera: Pieridae). *Journal of the New York Entomological Society* **100**: 311–319.

Shelley, R. M. 1990*a*. Revision of the milliped family Eurymerodesmidae (Polydesmida: Chelodesmidea). *Memoirs of the American Entomological Society* **37**: 1–112.

——— 1990*b*. Are allopatric/parapatric mosaic complexes widespread in the Diplopoda? *In*: Minelli, A., ed., *Proceedings of the 7th International Congress of Myriapodology*. Leiden: E. J. Brill. p. 23.

——— 1993. The milliped genus *Isaphe* Cook (Polydesmida: Xytodesmidae). *Canadian Journal of Zoology* **71**: 1161–1168.

——— 1995. The Sigmocheirini, a xytodesmid milliped tribe in the Sierra Nevada Mountains, California, U.S.A. (Polydesmida: Xytodesmidae). *Entomologica Scandinavica* **26**: 339–360.

——— 1996*a*. Revision of the milliped genus *Xystocheir* Cook (Polydesmida: Xytodesminae). *Canadian Journal of Zoology* **74**: 1336–1363.

——— 1996*b*. The milliped order Callipodida in western North America (Schizopetalidae: Tynommatinae) and a summary of the New World fauna. *Entomologica Scandinavica* **27**: 25–64.

——— 1997. A re-evaluation of the milliped genus *Motyxia* Chamberlin, with a re-diagnosis of the tribe Xystocheirini and remarks on the bioluminescence (Polydesmida: Xytodesmidae). *Insecta Mundi* **11**: 331–351.

——— 2001. A synopsis of the milliped genus *Aniulus* Chamberlin (Julida: Parajulidae: Parajulinae: Aniulini). *Texas Memorial Museum, Speleological Monographs* **5**: 73–94.

Shelley, R. M. & Whitehead, D. R. 1986. A reconsideration of the milliped genus *Sigmoria*, with a revision of *Deltotaria* and an analysis of the genera in the tribe Aphelorini. *Memoirs of the American Entomological Society* **35**: 1–223.

Shimizu, Y. & Ueshima, R. 2000. Historical biogeography and interspecific mtDNA introgression in *Euhadra peliomphala* (the Japanese land snail). *Heredity* **85**: 84–96.

Sota, T., Takami, Y., Kubota, K., Ujiie, M. & Ishikawa, R. 2000. Interspecific body size differentiation in species assemblages of the carabid subgenus *Ohomopterus* in Japan. *Population Ecology* **42**: 279–291.

Tanabe, T. & Shinohara, K. 1996. Revision of the millipede genus *Xystodesmus*, with reference to the status of the tribe Xystodesmini (Diplopoda: Xystodesmidae). *Journal of Natural History* **30**: 1459–1494.

Tanabe, T., Katakura, H. & Mawatari, S. F. 2001. Morphological difference and reproductive isolation: morphometrics in the milipede *Parafontaria tonominea* and its allied forms. *Biological Journal of the Linnean Society* **72**: 249–264.

Wehner, R., Wehner, S. & Agosti, D. 1994. Patterns of biogeographic distribution within the *bicolor* species group of the North African desert ant, *Cataglyphis* Foerster 1850 (Insecta: Hymenoptera: Formicidae). *Senckenbergiana Biologica* **74**: 163–191.

Wiley, E. O. 1978. The evolutionary species concept reconsidered. *Systematic Zoology* **27**: 17–26.